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INVESTIGATIONS ON THE PHYLOGENY OF THE ANGIOSPERMS

3. NODAL ANATOMY AND THE MORPHOLOGY OF STIPULES

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The morphology of stipules has been a much debated subject since careful study of plant structures began. These generally small and inconspicuous appendages at the base of the petiole, which occur so constantly in some families of angiosperms and which are so invariably absent in others, have been regarded variously as "accessory leaves," as independent organs, as a "product of the leaf base of the primordial leaf," as the remains of the two lateral leaflets of a three-compound leaf, as an incomplete axillary ligule, as a reduced leaf-sheath or as the remains of such a sheath of fused leaves as occurs in Equisetum. Almost everyone who has written on the subject has had a different idea as to just what the nature of stipules is and what has been the cause of their origin; and the relations between stipules, leaf-sheath, ligule, tendril, petiolar spine and ochrea have been widely discussed by many botanists. The following paper has as its object a presentation of certain anatomical facts, apparently overlooked hitherto, which seem to be of importance in connection with this general problem.

One of the writers (3) has recently made a comparative study of the anatomy of the node throughout the angiosperms and has come to certain conclusions as to the evolutionary development of the various types of nodal structure in that group. The facts and conclusions in his paper may be briefly summarized as follows.

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1. In vascular plants below the Gnetales and angiosperms the foliar trace, whether it is a single bundle or is composed of two or of many strands, causes at its departure only a single break or gap (if any) in the continuity of the woody ring of the stem.

2. Among angiosperms the nodal topography is much more various for there may be a single gap (unilacunar type), three distinct and usually distant gaps (trilacunar type), or many gaps (multilacunar type). The nodal plan is exceedingly constant within large groups, most families and many orders being almost invariably characterized by some one of the three types.

3. From its predominance in the lower Archichlamydeae and especially in the presumably primitive Amentiferae, Ranales and Rosales, and from its occurrence in the more primitive members of otherwise unilacunar or multilacunar families or orders, the trilacunar type is regarded as the most ancient angiosperm condition.

4. The unilacunar node has evidently been derived by a reduction of the trilacunar, either through the approximation of the three gaps and their coalescence into one; or through the disappearance of the two lateral bundles and gaps.

5. The multilacunar type has been derived by an amplification of the three original bundles and gaps into five, seven, nine or more.

6. The multilacunar node of the monocotyledons has apparently been derived from such a trilacunar condition as persists in the Potamogetonaceae and in the seedlings of other families.

The importance of these facts of nodal anatomy in connection with the morphology of stipules, sheathing leaf-bases and related structures is evident when we observe that *in the majority of plants with a trilacunar node, stipules are present; that in almost all with a unilacunar node, stipules are absent, and that in all with a multilacunar node, the leaf has a more or less sheathing base.* There is obviously an intimate connection between the type of nodal topography and the occurrence of stipules.

The following table[1] indicates briefly the facts as to the occurrence of stipules and related structures in the more important families of dicotyledons, together with the prevailing type of nodal topography (and and also of leaf margin) in each.

[1] Parentheses indicate an uncommon condition. The three types of nodal topography are represented by the figures 1, 3 and ∞. The prevailing character of the leaf margin in each family is noted in cases where both types are not well represented.

Family	Stipules	Node	Margin
Casuarinaceae	0	1	Entire
Piperaceae	+ or 0	3 or ∞	Entire
Chloranthaceae	+	3 or ∞	Toothed
Salicaceae	+	3	Toothed
Garryaceae	0	3	Entire
Myricaceae	+ or 0	3 or 1	Both
Leitneriaceae	0	3	Entire
Juglandaceae	0	3(5)	Both
Julianaceae	0	3	Entire
Betulaceae	+	3	Toothed
Fagaceae	+	3	Toothed
Ulmaceae	+	3	Toothed
Urticaceae	+	3	Toothed
Moraceae	+ or Sheath	3 or ∞	Entire
Proteaceae	0	3	Toothed
Santalaceae	0	1	Entire
Olacaceae	0	3	Entire
Loranthaceae	0	1	Entire
Aristolochiaceae	0	3	Entire
Polygonaceae	Sheath	∞	Entire
Chenopodiaceae	0	1	Entire
Amarantaceae	0	1	Entire
Nyctaginaceae	0	1	Entire
Phytolaccaceae	0	1	Entire
Aizoaceae	0, (+)	1	Entire
Portulacaceae	+	1	Entire
Caryophyllaceae	0, (+)	1	Entire
Trochodendraceae	+ or 0	1, 3, 5	Toothed
Ranunculaceae	+ or Sheath	3 or ∞	Toothed
Lardizabalaceae	0	3	Entire
Berberidaceae	+	3 or ∞	Toothed
Menispermaceae	0	3	Entire
Magnoliaceae	+, 0, or Sheath	3, 1, or ∞	Entire
Calycanthaceae	0	3	Entire
Anonaceae	0	1	Entire
Myristicaceae	0	1	Entire
Monimiaceae	0	1	Both
Lauraceae	0	1	Entire
Hernandiaceae	0	1	Entire
Papaveraceae	0, (+) or Sheath	3 or 1	Toothed
Capparidaceae	+ or 0	1	Entire
Cruciferae	0	3 or 1	Both
Resedaceae	Minute	1	Both
Crassulaceae	0	3 or 1	Entire
Saxifragaceae	+ or 0	3, (5)	Toothed
Pittosporaceae	0	3	Entire
Cunoniaceae	+	3	Toothed
Hamamelidaceae	+	3	Both
Platanaceae	+	7	Toothed
Crossosomataceae	0	3	Entire
Rosaceae	+, (0)	3, (1, 5)	Toothed
Connaraceae	0	3	Entire
Leguminosae	+	3, (5)	Entire

Family	Stipules	Node	Margin
Geraniaceae	+ or o	3	Toothed
Oxalidaceae	o, (+)	3	Entire
Tropaeolaceae	o, (+)	3	Both
Linaceae	+ or o	3	Both
Zygophyllaceae	+	3	Entire
Rutaceae	o, (+)	3, (1)	Entire
Simarubaceae	o	7	Entire
Burseraceae	o, (+)	5	Entire
Meliaceae	o	5	Entire
Malpighiaceae	+	3, (1)	Entire
Vochysiaceae	o, (+)	1	Entire
Tremandraceae	o	1	Entire
Polygalaceae	o	1	Entire
Euphorbiaceae	+ or o	3, (1)	Both
Buxaceae	o	1	Entire
Empetraceae	o	1	Entire
Coriariaceae	o	1	Entire
Anacardiaceae	o, (+)	3	Both
Cyrillaceae	o	1	Entire
Aquifoliaceae	o, (+)	3, (1)	Both
Celastraceae	Minute or o	1	Toothed
Staphylleaceae	+	3	Both
Aceraceae	o	3	Toothed
Hippocastanaceae	o	3, (5)	Toothed
Sapindaceae	+ or o	3	Both
Balsaminaceae	o	1	Toothed
Rhamnaceae	+	3	Both
Vitaceae	+	3, 5, 7	Toothed
Elaeocarpaceae	+	3	Both
Tiliaceae	+	3	Toothed
Malvaceae	+	3, (∞)	Toothed
Sterculiaceae	+	3	Both
Dilleniaceae	+ or o	3 or 1	Both
Eucryphiaceae	+	3	Toothed
Ochnaceae	+	3	Toothed
Marcgraviaceae	o	1	Entire
Theaceae	o	1	Both
Guttiferae	o, (+)	1	Entire
Dipterocarpaceae	+	3 or 5	Entire
Cistaceae	+ or o	1	Entire
Bixaceae	+	3	Toothed
Violaceae	+	3	Toothed
Flacourtiaceae	+	3	Both
Stachyuraceae	+	3	Toothed
Passifloraceae	+	3	Both
Caricaceae	o	3 or ∞	Toothed
Begoniaceae	+	3	Toothed
Peneaceae	Minute	1	Entire
Oliniaceae	o	1	Entire
Thymeleaceae	o	1	Entire
Eleagnaceae	o	1	Entire
Lythraceae	Minute or o	1	Entire
Punicaceae	o	1	Entire

Family	Stipules	Node	Margin
Lecythidaceae	0	1	Entire
Rhizophoraceae	+	3	Entire
Nyssaceae	0	3	Entire
Alangiacae	0	3	Entire
Combretaceae	0	1	Entire
Myrtaceae	0	1	Entire
Melastomataceae	0	1	Entire
Oenotheraceae	0, (+)	1	Both
Araliaceae	Sheath	∞	Both
Umbelliferae	Sheath	∞	Toothed
Cornaceae	0	3	Entire
Clethraceae	0	1	Toothed
Pirolaceae	0	1	Both
Ericaceae	0	1	Entire
Epacridaceae	Sheath	∞	Entire
Diapensiaceae	0	1	Both
Theophrastaceae	0	1	Both
Myrsinaceae	0	1	Entire
Primulaceae	0	1	Both
Plumbaginaceae	+ or Sheath	3	Entire
Sapotaceae	0, (+)	1	Entire
Ebenaceae	0	1	Entire
Symplocaceae	0	1	Toothed
Styracaceae	0	1	Entire
Oleaceae	0	1	Entire
Loganiaceae	+ or 0	1	Both
Gentianaceae	0 or Sheath	1 or ∞	Entire
Apocynaceae	0, (+)	1	Entire
Asclepiadaceae	0	1	Entire
Convolvulaceae	0, (+)	1	Entire
Polemoniaceae	0	1	Entire
Hydrophyllaceae	0	1	Entire
Borraginaceae	0	1	Entire
Verbenaceae	0	1	Both
Labiatae	0	1	Toothed
Solanaceae	0	1	Both
Scrophulariaceae	0	1	Both
Bignoniaceae	0	1	Entire
Gesneraceae	0	1, (3)	Both
Acanthaceae	0	1	Entire
Myoporaceae	0	1	Entire
Plantaginaceae	0	3	Both
Rubiaceae	+	1, (3)	Entire
Caprifoliaceae	+ or 0	3, (5)	Both
Valerianaceae	0	3	Both
Dipsacaceae	0	3	Toothed
Cucurbitaceae	0	3	Toothed
Campanulaceae	0	1	Both
Goodeniaceae	0	3 or 5	Both
Compositae	+ or 0	3 or ∞	Both

A perusal of this table makes plain the following facts. Of the 75 families which possess stipules or leaf sheaths, 53 are characteristically tri- or multilacunar and in 5 others this type of node is very common. 16 of these stipulate families are characteristically unilacunar, but in 11 of them stipules are either very rare or minute, and in the others (Portulacaceae, Capparidaceae, Cistaceae, Loganiaceae and Rubiaceae) they are often poorly developed or absent. Of the 81 families, on the other hand, which are totally without stipules 52 are characteristically unilacunar and 2 more are frequently so; and 27 have three or more traces. Of the 78 typically tri- or multilacunar families, 53 have stipules. Of the 70 typically unilacunar ones, 57 are without stipules and in the other 13 these structures are usually rare or inconspicuous. The families in which the leaf base is characteristically sheathing, such as the Polygonaceae, Araliaceae and Umbelliferae, practically always have a multilacunar node. It is thus apparent that stipules and lateral leaf traces generally occur together. The exceptions to this rule will be discussed later.

The following particular cases are of interest in showing the relation between nodal anatomy and the presence of stipules.

The Polygonaceae are prevailingly multilacunar and in almost every case possess a stipular structure, the ochrea, which completely encircles the stem. The dioecious species of Rumex, however, are exceptional in the family in having a trilacunar node and also in possessing two typical and distinct stipules instead of an ochrea.

The Aquifoliaceae are generally unilacunar and stipules are either absent or very small among them. In *Ilex opaca*, however, which has two lateral traces and gaps, the stipules reach their best development in the family.

The Rosaceae are typically trilacunar and stipulate. Spiraea and its allies, however, are exceptional in being unilacunar and also exstipulate.

Certain genera of the Dilleniaceae are trilacunar and others unilacunar. Stipules are generally absent in the family, but the few cases where they occur are only in the trilacunar genera.

Almost all of the Umbelliferae are multilacunar and have sheathing leaf-bases. Hydrocotyle, however, is exceptional in being trilacunar and in having two typical and distinct stipules.

The intimate connection between stipules and the two lateral bundles of a trilacunar leaf-trace is therefore very apparent. A study

of the nodal anatomy suggests an explanation for this fact, for the stipules are invariably inserted directly opposite the points of origin of the two lateral bundles (*figs.* 1, 4 and 5), really as continuations of the two swellings on the surface of the stem caused by the exit of the traces. If we go back to the primordium of such a leaf at the growing point we find that it usually begins as a three-lobed structure, the central lobe giving rise to the petiole and blade and the lateral ones to the stipules. These three lobes mark the future position of the three leaf-traces. In subsequent development the stipules usually grow considerably, often equalling or exceeding the young blade for a time (*fig.* 2), and still showing their relation to the three swellings which mark the position of the procambial strands that are to give rise to the leaf-traces. The traces, however, when they are finally formed, do not enter the three primordial lobes of the leaf but all three converge into the central one, which is to form the petiole and blade. Each stipule obtains its vascular supply, if it has one, from branches derived from the corresponding lateral traces (*figs.* 1 and 5). These facts as to the topography of the vascular system at the base of the petiole and as to the innervation of the stipules have been worked out by numerous investigators, particularly by Colomb (1). He makes the origin of the vascular supply to the stipules their most distinguishing character and defines a stipule as "an appendage inserted on the stem at the base of the leaf, all the bundles of which are derived entirely from the corresponding foliar bundles."

The significant fact, however, seems to be the intimate connection between the stipules and the swellings opposite the lateral leaf-traces This is even manifest in the case of stipules which are adnate to the petiole for a considerable distance, as in certain of the Rosaceae and many other plants; for here the base of the free portion of each stipule (its oldest part) is directly opposite the point of origin of one of the lateral traces (*fig.* 3), although the subsequent growth of the basal portion of the leaf (*a–b*) carries the stipules up and renders their connection with the lateral bundles, except in very young leaves, less obvious. In a unilacunar node there is of course only one swelling (*fig.* 6) and this developes directly into the petiole and blade without an accompanying formation of stipules. All these facts suggest the conclusion that the early growth of the tissue which is to form the lateral traces exerts a stimulating influence which results in the formation of a considerable body of tissue, the stipule. It is almost as if a

whole leaf began to be developed opposite each departing trace (as in the lower vascular plants) but that only the middle one persisted. There certainly appears to be some sort of morphogenetic connection between lateral leaf-trace and stipule.

In the case of sheathing leaf bases and the polygonaceous ochrea we really have a row of adjacent stipules (each opposite one of the numerous leaf-trace bundles) which have become fused together. Sometimes, especially in the case of five-bundle nodes, there are two broad-based stipules, as in most of the Vitaceae, each opposite a pair of traces. When the bundles and gaps are more numerous and occur round most of the stem periphery, as in the Umbelliferae and many others, the sheath is much broader and its resemblance to two stipules is usually gone; but even in such cases it occasionally manifests itself, as in certain of the Magnoliaceae.

The relation between the stipules of dicotyledons, on the one hand, and the ligule of grasses, the tendril of Smilax and the "stipules" of the Potamogetonaceae, on the other, has been much discussed. A study of the nodal anatomy of these monocotyledonous plants and its relation to the appendages in question is helpful in determining their real nature.

In the more vigorous species of the Potamogetonaceae, a family which modern classifications regard as among the most primitive of monocotyledons, three main bundles enter the base of the leaf just as in the trilacunar dicotyledons, a much simpler condition than that prevailing in most monocotyledons. From the two lateral ones branches are sent off into the stipules (*fig.* 7), so that these organs receive their vascular supply in precisely the same way as do the dicotyledonous stipules. On the basis of this evidence the two structures certainly appear to be homologous. It is significant that both in their nodal anatomy and in the character of their stipular appendages the Potamogetonaceae approach the dicotyledons more closely than do any other monocotyledons.

The two tendrils of Smilax, which are inserted at the base of the petiole, are apparently homologous with the stipules of the Potamogetonaceae, for their vascular supply is largely derived from the lateral members of a trio of large bundles which, with a number of smaller ones, enter the base of the leaf from the axis.

The ligule of grasses, the vascular supply of which was investigated carefully by Colomb, is more complicated anatomically but seems to

be homologous with the stipular appendages of the other monocotyledons which we have discussed. Anatomical evidence therefore points toward a connection between nodal topography and stipular appendages in the monocotyledons similar to that which we have noted in the dicotyledons.

Let us now consider the various exceptions to the general rule that lateral leaf-traces and stipules always occur together.

There are about 20 unilacunar families in which stipules are found, but in most of these families they are rare and are almost always thin, scarious or minute. If our theory is correct, these unilacunar families have been derived by reduction from trilacunar (and hence presumably stipulate) ones, and it would therefore be only natural that stipules or vestiges of them should occasionally persist. In many cases the vascular supply of a unilacunar leaf, although causing but a single gap, is composed of three bundles; and the stipules, when present, are often related to the lateral ones of this trio. The interpetiolar stipule of the Rubiaceae is evidently to be regarded as a fusion of two formerly independent and adjacent ones, since each stipule receives its vascular supply from both leaf-traces.

There are also about 30 families which are prevailingly trilacunar but in which stipules are absent or rare. Some of the more important of these are the Juglandaceae, Proteaceae, Menispermaceae, Aristolochiaceae, Lardizabalaceae, Calycanthaceae, Pittosporaceae, Simarubaceae, Burseraceae, Meliaceae, Aceraceae, Plantaginaceae and Cucurbitaceae.[2] Many genera and species in normally stipulate, trilacunar families often lack stipules. The lateral bundles at the node in such plants do not cause the formation of stipules, but directly opposite each lateral trace is often observable a swelling or rounded projection which only needs to be slightly elongated, or to be the seat of a gland or water pore, to become a typical stipule.

If we examine these exstipulate trilacunar families, as set forth in the previous table, we are at once struck by the fact that in the great majority of them (about 75 per cent) the leaves or leaflets are prevailingly *entire*. This suggests the possibility that stipules, on the one hand, and the teeth or lobes of the lamina, on the other, may be dependent for their occurrence on essentially the same factor or factors.

Such an hypothesis is strengthened by a study of the relation

[2] The tendrils of the Cucurbitaceae are perhaps stipular in character.

between the character of the leaf margin and the occurrence of stipules in those families which have both toothed and entire, and stipulate and exstipulate, leaves. In the Saxifragaceae, for example, the entire-leaved genera Philadelphus, Deutzia and Hydrangea are without stipules, whereas stipules or stipule-like appendages occur in Ribes, which almost always has toothed leaves; and also in certain of the herbaceous serrate genera. In the Caprifoliaceae the entire-leaved genera Lonicera and Diervilla are exstipulate, as are the entire-leaved species of Viburnum, but the serrate, dentate or lobed species of the last-named genus are in the great majority of cases provided with stipules. The Rosaceae are overwhelmingly stipulate, but in the sub-family Chrysobalanoideae, which is mainly tropical and entire-leaved, stipules are either absent or extremely small. The same fact is also evident within single genera, for those species of Salix, for example, which are quite entire, have no stipules or have very small ones; and *Myrica asplenifolia*, with its strongly dentate leaves, is stipulate whereas the other species, many of which are nearly or quite entire, are not provided with stipules. In all these instances the node is trilacunar. In many other families, such as the Euphorbiaceae, Violaceae, Moraceae and others, the absence or small size of stipules in entire-leaved species and their strong development in species with toothed leaves is evident.

The resemblance between stipules and leaf-teeth is still further emphasized by the fact that in the young leaf both structures are almost always tipped with water pores or with glands, and that these pores or glands usually become functionless in the mature leaf. Stipules in many cases wither and fall when the leaf comes to maturity. The facts seem to point to a similar functional importance, in the young and growing leaf, of the terminal organs of both stipules and teeth, a function which usually ceases after the leaf has become mature.

The occurrence of stipules therefore seems to be dependent on the structure of both the node and the margin. When the node is trilacunar and the margin toothed, stipules are almost invariably present; and when the node is unilacunar and the margin entire, they are almost invariably absent. The former determining factor is evidently the more important of the two, for the presence of lateral traces seems to be almost essential to the production of stipules, often causing them to be developed in plants the leaves of which are devoid of marginal pores or glands. The presence of such a pore or gland,

however, usually seems to be necessary for the production of a definite stipular appendage instead of a mere rounded swelling.

What light, then, do these anatomical facts throw on the vexed question of the morphology of stipules? They lend little support to the theories that these structures are independent organs, vestiges of a sheath of fused leaves or lateral leaflets of a compound leaf, but rather favor the contention that stipules are integral portions of the base of the leaf, a view which is well expressed by Eichler when he says that stipules arise without exception as a product of the leaf-base of the primordial leaf. Anatomical facts are also in agreement with the theory frequently put forward that stipules, the sheathing leaf-base, the ochrea, the stipular appendages of the lower monocotyledons and the tendrils and ligule of the higher ones are morphologically identical, for the character and position of these various structures is to a large extent dependent on the type of nodal topography and the manner in which the base of the leaf is innervated. The so-called stipules of ferns and gymnosperms are not dependent on nodal anatomy and are therefore apparently not to be regarded as homologous with those of angiosperms.

As to just what is the morphological character of stipules we cannot be quite sure, but the results of the present investigation indicate that they may perhaps be considered as the two earliest leaf-teeth, their position being determined by that of the two lateral traces rather than by that of the vascular bundles of the lamina, as in the case of ordinary teeth. They may also be regarded as two basal leaf lobes, although the difference between a tooth and a lobe seems to be more one of degree than of kind. The function of stipules as bud scales in certain families apparently does not indicate their true morphological nature but is rather to be looked upon as a secondary adaptation.

As to the phylogeny of stipules there seems to be considerable doubt. The bulk of opinion, expressed by many writers and recently emphasized by Domin (2) in a series of papers, is that a ligule or sheathing leaf-base is the most primitive condition and that this has gradually degenerated, in many families of dicotyledons, into two stipules. The facts brought forward in the present paper show that the character of the leaf-base, whether sheathing, stipulate or devoid of appendages, depends closely upon whether the node is multilacunar, trilacunar or unilacunar, respectively. The question as to which

type of leaf-base is the most ancient is therefore intimately connected with the parallel question as to which type of nodal anatomy is the most ancient. In a previous paper one of the writers has brought forward evidence that the trilacunar node is the most primitive angiosperm condition. If this theory is the correct one a leaf with two independent stipules is evidently more ancient in type than one with a sheathing base, the latter having arisen by an increase in basal extent of the stipules and their gradual fusion with the petiole.

As to whether the earliest angiosperms were provided with stipules or not we may not be sure. If the leaf margins of these plants were devoid of glands or pores, it is very likely that rounded swellings, rather than typical stipules, occurred opposite the lateral leaf-traces, as in the trilacunar entire families today. On the other hand, if primitive angiosperms possessed toothed leaves, it seems altogether probable that they were provided with stipules from the first. The fact that in so many families of plants stipules bear evidences of reduction would rather indicate that they once were a much more conspicuous feature of angiosperm leaves than they generally are at present.

Summary

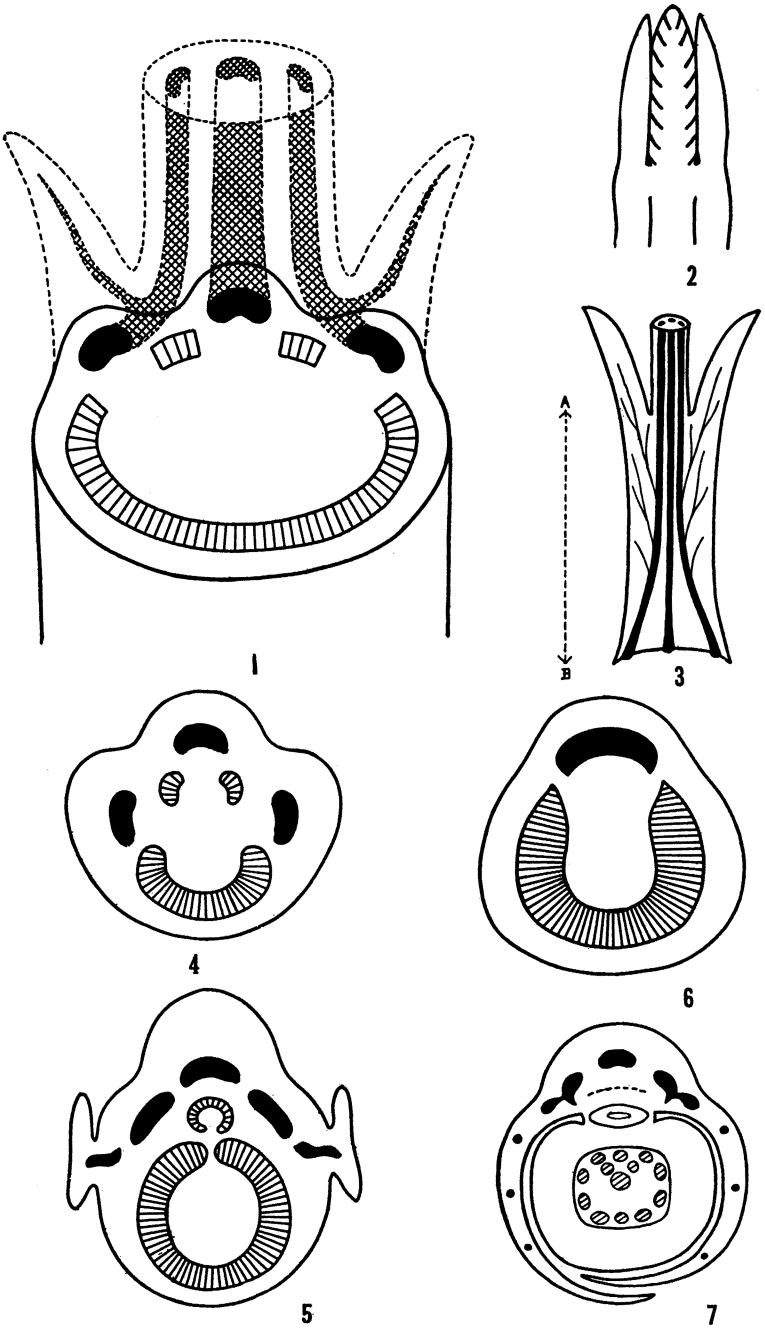
1. There is an intimate connection between the type of nodal anatomy (one, three or many traces and gaps) and the occurrence of stipules and similar structures in dicotyledons. In the majority of plants with a trilacunar node stipules are present; in almost all with a unilacunar node they are absent, and in all with a multilacunar node the leaf has a sheathing base.

2. There is a similar connection in monocotyledons, particularly in such primitive forms as the Potamogetonaceae.

3. The growth of the lateral leaf-trace apparently exerts a stimulus which results in the development of the stipule, for the stipule invariably occurs directly opposite the point of departure of the trace.

4. The character of the leaf margin is also important in governing the occurrence of stipules, for stipules are generally absent in entire-leaves families, even though the latter are trilacunar. The fact that stipules and leaf teeth almost always possess apical pores or glands which are usually atrophied after the leaf has reached maturity suggests that both structures have essentially the same function.

5. Morphologically, stipules are to be regarded as integral portions of the leaf, and seem to be more nearly homologous with teeth than



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with any other structures. Stipules, sheaths, ligules and similar modifications of the base of the petiole are dependent in position and character on the anatomy of the node, and seem thus to be essentially homologous.

6. A leaf provided with two distinct stipules is more ancient in type than one with a sheathing base.

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DESCRIPTION OF FIGURES OF PLATE XLIV.

FIG. 1. Diagram showing relation of stipules to lateral leaf-traces and course of traces in the base of the petiole.

FIG. 2. Very young leaf of Robinia, showing stipules and blade.

FIG. 3. Base of petiole of Rosa showing relation of free portions of stipules to insertion of lateral leaf-trace bundles.

FIG. 4. Transverse section just below node of Hamamelis (typical trilacunar dicotyledon) showing departure of the three leaf-traces and the swellings opposite them.

FIG. 5. Transverse section a little higher up than in *fig.* 4, showing the formation and innervation of the stipules.

FIG. 6. Transverse section at the node of Eucalyptus (typical unilacunar dicotyledon) showing absence of lateral leaf-traces and stipular swellings.

FIG. 7. Transverse section at node of Potamogeton showing general nodal topography, with formation and innervation of stipules.